SMALL-SCALE MOVEMENTS OF LOBSTERS (*HOMARUS AMERICANUS*): AN APPLICATION OF RADIO-ACOUSTIC POSITIONING AND TELEMETRY (RAPT) WITH AN ANALYSIS OF SYSTEM RESOLUTION

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by

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ABSTRACT

Five female lobsters (*Homarus americanus*) were tagged with ultrasonic pingers and tracked with a 3-buoy system over a 2-week period using radio-acoustic positioning and telemetry (RAPT). Simulation analysis of positioning errors showed that the error distribution was anisotropic and elliptical in shape. The errors increased with distance from the centre of the triangle formed by the buoys. Inside the triangle the error in the radial direction was less than $\pm$ 2 m. This error component was $\pm$ 4 m at 150 m from the centre of the buoy array, and $\pm$ 7 m at 200 m from the centre. Buoy movements due to wind and current contributed approximately 90% of the error. Two of the lobsters were tracked throughout the period with the mean number of position fixes $\geq$ 99 per day. The remaining three lobsters either left the area completely or came into the range of the system to provide a series of positions on 2-3 days. The two lobsters occupied overlapping territories of approximately 100 m diameter over the 2-weeks. Distances traveled over 24-h periods by the two lobsters averaged 278 and 350 m but were greater at night (means of 188 and 267 m between 2000-0700 hr), than during day (means of 90 and 83 m between 0700-2000). Movement of the two lobsters was significantly correlated with light levels, but not with current. Lobsters appeared to reside in shelters during part of the day. The utility of RAPT for studying lobster behavior is demonstrated by the analysis of lobster behavior in the presence of baited traps on three nights. T here were five occasions when tagged lobsters were 10 m or less from a trap; a capture occurred only once.

RÉSUMÉ

Nous avons posé un émetteur d'ultasons à cinq homards femelles (*Homarus americanus*) que nous avons ensuite suivis par localisation/télémétrie radio-acoustique pendant deux semaines au moyen d'un dispositif de trois bouées. Selon l'analyse de simulation des erreurs de localisation, la distribution des erreurs était anisotrope et de forme elliptique. L'erreur augmentait avec la distance à partir du centre du triangle formé par les bouées. À l'intérieur du triangle, l'erreur sur l'axe radial était inférieure à $\pm$ 2 m. Cette erreur était de $\pm$ 4 m et de $\pm$ 7 m à 150 m et à 200 m du centre du triangle, respectivement. Environ 90 % de l'erreur était attribuable aux mouvements des bouées sous l'action du vent et des courants. Nous avons suivi deux des homards pendant toute la période de deux semaines, avec un nombre moyen d'au moins $\geq$ 99 localisations par jour. Les trois autres homards ont complètement quitté la zone ou n'ont été à la portée du dispositif pour être localisés pendant deux ou trois jours. Durant les deux semaines, les deux homards ont occupé des territoires chevauchants faisant environ 100 m de diamètre. Durant des périodes de 24 heures, les deux homards se sont déplacés sur des distances moyennes de 278 m et de 350 m; les distances parcourues étaient plus grandes la nuit (moyennes de 188 m et de 267 m de 20 h à 7 h) que le jour (moyennes de 90 m et de 83 m de 7 h à 20 h). Les déplacements des deux homards ont présenté une corrélation significative avec l'intensité lumineuse, mais pas avec les courants. Les homards semblaient occuper des abris pendant une partie du jour. L'analyse du comportement des homards en présence de casiers appâtés pendant trois nuits illustre l'utilité de la localisation/télémétrie radio-acoustique pour l'étude du comportement des homards. Un homard muni d'un émetteur s'est trouvé à 10 m ou moins d'un casier à cinq occasions, mais il n'y a eu qu'une seule capture.

INTRODUCTION

The ability to measure small-scale movement (meters to 10s of meters) of benthic animals is important to the study of behavior and habitat use. For animals that are fished by baited traps, such as the American lobster *Homarus americanus*, measuring small-scale movement would be valuable for examining behavioral reactions to the trap, and for estimating the area of attraction of baited traps (sensu Miller 1990). *In situ* studies of small-scale movement in the American lobster by diving (e.g. Stewart 1972; Ennis 1984a; Karnofsky et al. 1989) provide a wealth of information on behaviors related to shelter, foraging, social interactions and homing. However around the clock tracking of individual lobster movements in nature by diving is not practical.

Another approach for tracking individuals is via telemetry, either ultrasonic or electomagnetic. In ultrasonic telemetry, acoustic pressure transmitters ("pingers" or "ultrasonic tags") that are fixed to the animal create waves at ultrasonic frequencies. The ultrasonic signals are detected by hydrophones and receivers. Most previous reports of ultrasonic tracking of *Homarus americanus* (Lund and Lockwood 1970; Maynard and Conan 1984; Jarvis 1989; Watson et al. 1999) and other decapods (e.g. blue crab and spider crab - Hines et al. 1995) have tracked animals from small boats, which limit the spatial and temporal resolution. Lund et al. (1973) were able to quantify movements greater than 30 m; Jarvis (1989) and Watson et al. (1999) were able to measure changes in position of greater than 50 m. In these studies the animals were usually located less than 5 times per day. Although it is accepted that lobsters are primarily nocturnal (Cooper and Uzmann 1980; Ennis 1984b; Lawton 1987; Karnofsky et al. 1989), studies which tracked animals both during the day and night (Maynard and Conan 1984; Jarvis 1989) were unable to detect an effect of time of day on movement. This may be due to the low spatial and temporal resolution of the tracking systems used in those studies.

For higher resolution in both time and space, systems that do not require position fixes from boats, and provide automatic updates of pinger positions are needed. Radio-acoustic positioning telemetry (RAPT) is capable of high-resolution tracking of pelagic animals such as squid over areas greater than 300 m by 300 m (Sauer et al. 1997; O'Dor et al. 1998). In this system the hydrophones are attached to moored buoys, which transmit the signal to a shore-based receiver. Using the arrival times of the acoustic pulses from the pingers, the base station calculates the position of the pinger. Optimally the buoys do not move once moored, but wind and currents can cause buoy movement, which can reduce the spatial resolution associated with tracking ultrasonic-tagged animals.

One of the challenges with tracking benthic animals that inhabit cobble-boulder habitats (such as lobsters) is the potential for signal attenuation and reflection by the rocky substrate. Electromagnetic systems are less affected by reef habitats, but have limited range and require a network of seabed aerials (Jernakoff 1987, Smith et al. 1998). Using such a system it was clearly demonstrated that *Homarus gammarus* was more active at night, but the area studied was just 15 m by 35 m, and the distances moved by individual lobsters were not reported.

In a pilot study using RAPT to track lobsters (O'Dor and Webber 1991), four large (> 120 mm carapace length) ovigerous females were tracked for five days in July 1989, and estimated total distance moved varied from 1.5-15 km. This first generation system located animals only

every 20 minutes, and statistical analysis of the position data was not possible. The development of routines for post-analysis of acoustic data have led to significant improvements in the ability to validate pinger positions and to evaluate resolution (O'Dor et al. 1998). In addition, higher observation frequency has increased the chances of positioning the animal if it leaves a shelter only periodically. With improved resolution and reliability, lobster habitat use and behavior in relation to fishing gear can be studied. Lower resolution RAPT was recently able to position crabs in relation to baited traps (Skajaa et al. 1998).

In this paper we provide the first evaluation of the spatial resolution of ultrasonic tracking of lobsters. We model positioning error related to the movement of the moored acoustic buoys which in an ideal world would be fixed, but in the marine environment tend to swing on the moorings due to wind and currents. This paper builds on earlier analyses presented in O'Dor et al. (2000). High resolution RAPT reveals interesting new insights about small-scale movement and activity rhythms in *Homarus americanus*. We show a strong linkage between activity and light levels, and provide examples of lobster tracks in the presence of baited traps.

MATERIALS AND METHODS

Study area

Jeddore Harbour on Nova Scotia's eastern shore (Fig. 1) was chosen as the study site because of previous studies of lobster movement and larval distribution in the area (Jarvis 1989; Dibacco and Pringle 1992; O'Dor and Webber, 1991). Jeddore Harbour consists of two inner arms linked to the open ocean via a channel. Tides are semi-diurnal with a mean range of about 1 m. Lobster fishing occurs in the harbour from April-June, although the area has low landings per km^2 of lobster bottom relative to other areas of coastal Nova Scotia (Hudon 1994). SCUBA diving in the area revealed a bottom type of primarily mud-silt at depths of 3-10 m, with rocky reefs close to shore and adjacent to islands. Lobsters densities were not rigorously estimated, but few lobsters were observed while diving on the mud bottom, and densities of lobsters > 70 mm carapace length, were less than 0.5 per 100 m^2. In the reef habitat, lobsters were more cryptic and densities were more difficult to estimate.

Radio-acoustic positioning (RAPT) system

A RAPT base station manufactured by VEMCO (Shad Bay, NS) was established in a fish shed on Jeddore Harbour from July 10-24 1997 (Fig. 1). The base station communicated with three radio-acoustic positioning buoys arrayed in an equilateral triangle with sides approximately 250 m. Buoys were moored with a rope-chain-anchor system (O'Dor et al. 1998), to minimize horizontal movements. The length of the sides of the triangle formed by the buoys was checked acoustically every 1-4 hours. This involved a pinger on each buoy transmitting for a short period while the other two buoys "listened". The dimensions of the buoy triangle were measured in this way every 1-4 hours during the two week experiment (148 times). The resultant time series of measurements of the three sides of the buoy triangle were later used to estimate variation in buoy positions caused by water movement for input to a simulation model (see below).

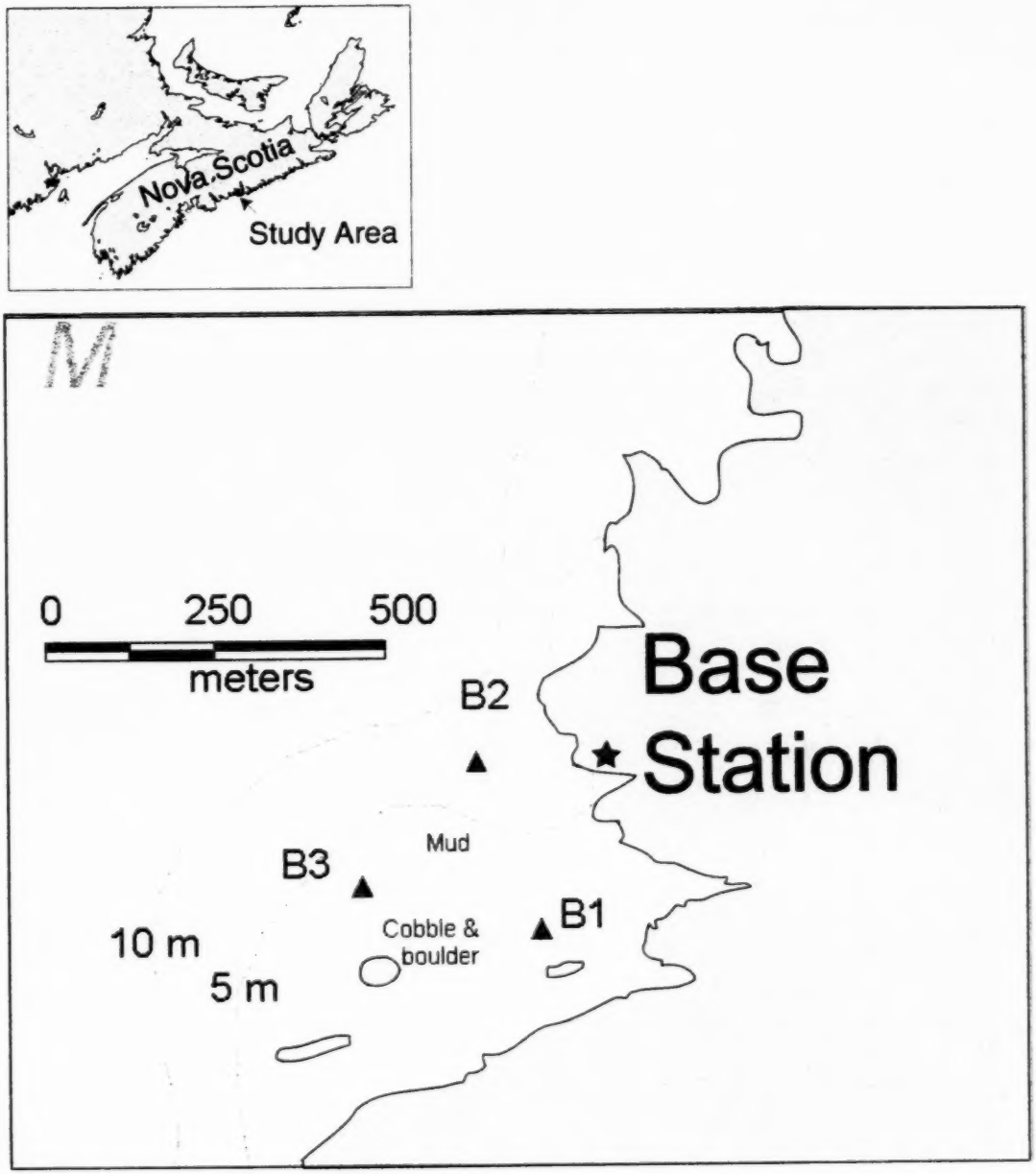

Fig. 1. Map of study area (Jeddore Harbour, N.S) showing location of buoys 1-3 (B1, B2, B3 indicated by triangles), base station. Also shown is bottom habitat in tracking area. Large "M" indicates mud

The calculation of pinger positions in RAPT systems is based on differences in the time for signals to reach the three buoys, together with knowledge of the speed of sound in water and the bottom depth in the study area. Pingers transmit on different frequencies so that they can be distinguished. In the RAPT system used in the present study, each pinger produced a pulse approximately every second. The buoys "listened" for one pinger for approximately 45 seconds and then sent the data to the base station in "packets" of signal arrival times (up to 45 individual pulses). The buoys then cycled through the remaining pingers. This cycle took 3-7 minutes depending upon the total number of active pingers. Maximum data recovery would occur if each buoy received all 45 pulses during each listening period over the two week experiment. As in most ultrasonic tracking studies, each buoy received only a subset of the total number of possible pulses because of signal attenuation, background noise, and because animals carrying the pingers move out of range.

Lobsters, pinger tags, and trapping

Five non-ovigerous female lobsters ranging in size from 72-85 mm carapace length, trapped within or adjacent to the buoy array, were tagged with VEMCO V-16 pingers using nylon cable-tie harnesses (Jarvis 1989), and released inside the array (Table 1).

Table 1. Pinger numbers, deployments on lobsters and fixed anchor and traps, and recovered data. Recovered data represents number of realized positions as a fraction of the number of potential positions (every 3-7 minutes during deployment depending on the number of active pingers). *For both deployments. CL = carapace length.

Pinger number	Attached to:	Description	Date	No days deployed	Recovered Data (%)
1	Lobster 1	73 mm CL female	July 11	13.0	68.8
2	Lobster 2	74 mm CL female	July 11	12.6	63.6
3	Lobster 3	72 mm CL female	July 11	12.6	22.2
4	Lobster 4	89 mm CL female	July 15	8.8	9.5
5	Lobster 5	86 mm CL female	July 15	7.7	0.7
6	Fixed anchor	Reference pinger - middle of array	July 11	13.0*	85.4*
	Trap 2	Baited lobster trap	July 22		
7	Trap 1	Baited lobster trap	July 21	2.9	87.0

The pingers were cylinders 58 mm long and 16 mm in diameter. Pinger weight (9-11 g in water) represented 5-9% of the lobsters body weight. Additional "reference" pingers were deployed in fixed locations to measure the spatial resolution of the system. Any variation in the calculated positions of reference pingers was attributed to positioning error. A single reference pinger was initially attached to an anchor in the centre of the buoy array; later this pinger and a second reference pinger were attached to two lobster traps. The baited lobster traps were set in the vicinity of the tagged lobsters on the last 3 days of the tracking

experiment to study trap-related behaviour. Three overnight sessions of lobster movement in the presence of baited traps were recorded. At the end of the experiment, 10 traps were placed in the area in an attempt to retrieve lobsters with pingers, and to roughly estimate the number of lobsters in the tracking area from the catch rate. The traps were 91 cm long by 53 cm wide by 36 cm high with two compartments ("kitchen" and "parlour"), constructed of plastic coated wire mesh with 3.8 cm mesh openings. Entrance ring diameters were 12.7 cm and there were no escape vents to allow release of small lobsters. Each trap was baited with 0.5 kg of frozen mackerel, placed in wire mesh bait boxes.

Light, currents and temperature

Bottom light, current speed and temperature were measured with a diver-deployed instrument described by Miller et al. (1996). Data were recorded every 15 minutes from July 16-24. The unit was deployed on the bottom at a depth of 4 m on the perimeter of the buoy array.

Post-analysis of RAPT tracking data

VEMCO's RAPT system software (versions 3.04 and later) records processed data to one file, and raw radio-transmitted data to another file. The processed data files contain positions calculated in real-time from packets of signal arrival times transmitted by each buoy to the base station. Buoy times are synchronized to base station time and signals are aligned in "triplets" (one pulse from one pinger received by each of the three buoys). The differences between arrival times are combined with buoy co-ordinates from an autopositioning routine to solve a set of hyperbolic equations to yield a position fix recorded in the processed data file. Thus a single position is derived for a given pinger from three packets of acoustic data (one from each buoy approximately every 3-7 minutes). Because the program must calculate, plot and save data arriving from a number of transmitters in real time, there is a limit to how sophisticated the analysis can be. With the raw radio-transmitted data, a more detailed analysis is possible including position verification and analysis of resolution.

Position resolution and buoy movement

Position calculations of the RAPT system are based on two assumptions: 1) the speed of sound in seawater is constant, isotropic and known and, 2) buoy positions are exactly known. Time differences are translated into distances and given the second assumption, the problem of calculating positions from time difference measurements reduces to a standard (but complex) geometry problem. We know that the second assumption was not met because although the buoys were moored, wind and water movements caused them to swing on their moorings. This introduces error into the calculated positions. To model this effect an estimate of the variance of buoy movement was needed. A test of the three time series of distances between buoys (see Radio-acoustic positioning RAPT System) against Normality indicated that they followed a Gaussian distribution, with an almost identical variance of approximately 1.44 m^2. This is consistent with similar positional variability among buoys. To model the error on calculated pinger positions caused by buoy movements, the following simulation procedures were used. First simulated buoy locations were established in a gridded reference system with squares of 5 m by 5 m. Next a model pinger was set and allowed to

transmit 600 times at each corner of the grid squares. The regions where the hyperbolae had two intersections (double solution regions) were not included in the simulation. Before measuring the distances from pinger to buoy, the buoys were displaced randomly from a Gaussian distribution with a variance of 1.44 m^2. Next the distances were transformed into arrival times and processed by the calculating algorithm. The simulation was completed by calculating the principal components of the distribution of calculated pinger positions for each corner of the grid squares. All data were processed under MATLAB® 5.1 and, the intricate sets of equations were solved using Maple® V.

RESULTS

Data recovery for the seven pingers ranged from 1-87% over the 13 days, with the fixed pingers (Pingers 6 and 7) providing the highest recovery rates (Table 1). Of the 5 tagged lobsters, Lobsters 1 and 2 remained in the range of the RAPT system for the entire period. For these lobsters the mean number of position fixes per day were 99 and 136. The remaining three lobsters either left the area completely or came into the range of the system to provide a series of positions on 2-3 days. Signals for the animals remaining in the area typically disappeared for several hours each day, mainly during daylight. Analysis suggests the animals did not leave the area during these hours, but instead entered shelters (see below).

Model of position resolution and comparison with fixed pingers

The simulation of positional errors caused by undetected buoy movements indicated that the error variance was anisotropic, with the magnitude of the error at each point on the grid depending on the direction (Fig. 2). As such the error was best represented by an ellipse instead of a circle (as in the case of isotropic error). The aspect ratio of the error ellipse was of the order of five with the long axis oriented in the radial direction. The errors increased with distance from the centre of the triangle formed by the buoys. Inside the triangle the error in the radial direction was less than $\pm$ 2 m. This error component was $\pm$ 4 m at 150 m from the centre of the buoy array, and $\pm$ 7 m at 200 m from the centre.

The simulated error ellipses agree well with the observed errors in the locations of the fixed reference pingers (Fig. 3). The spread of the points for fixed pingers in Fig. 3 is indicative of positioning error since with no error, all calculated positions for a fixed pinger would be identical. This was not the case because of the buoy movements. The elliptical shape of the calculated positions for fixed pingers and their orientation are in good accordance with the spread of the observed positions (Fig. 3). Note that while the simulated error ellipses represent one standard deviation in each direction, the observed positions are based on all available acoustic data. The final calculated position for the trap would be the centre of the ellipse. The simulation indicates that the error contribution by buoy movements is on the order of 90%.

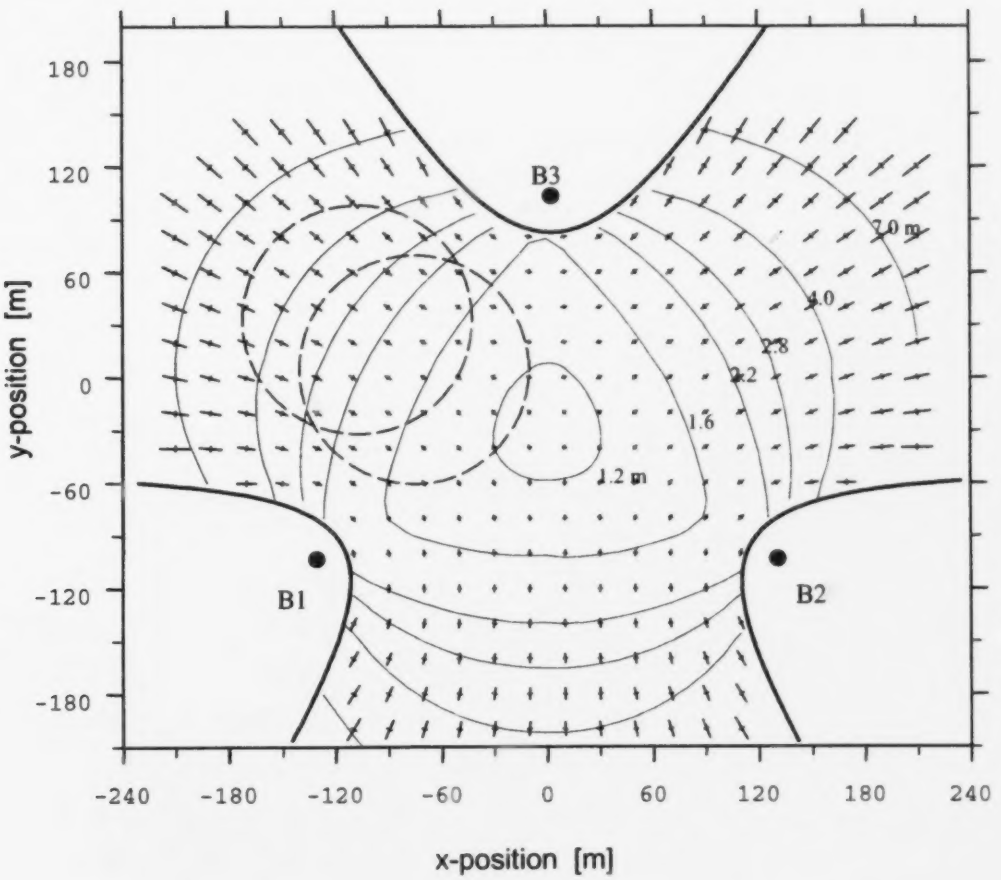

Fig. 2. Contour plot of positional errors caused by buoy movements derived from a simulation model described in the text. Each "cross" within the grid matrix shows the two major axes of the ellipses that describe positional errors. One standard deviation is shown for each axis. Also shown are buoy positions, double solution regions (behind each buoy) and estimated territories for Lobsters 1 and 2.

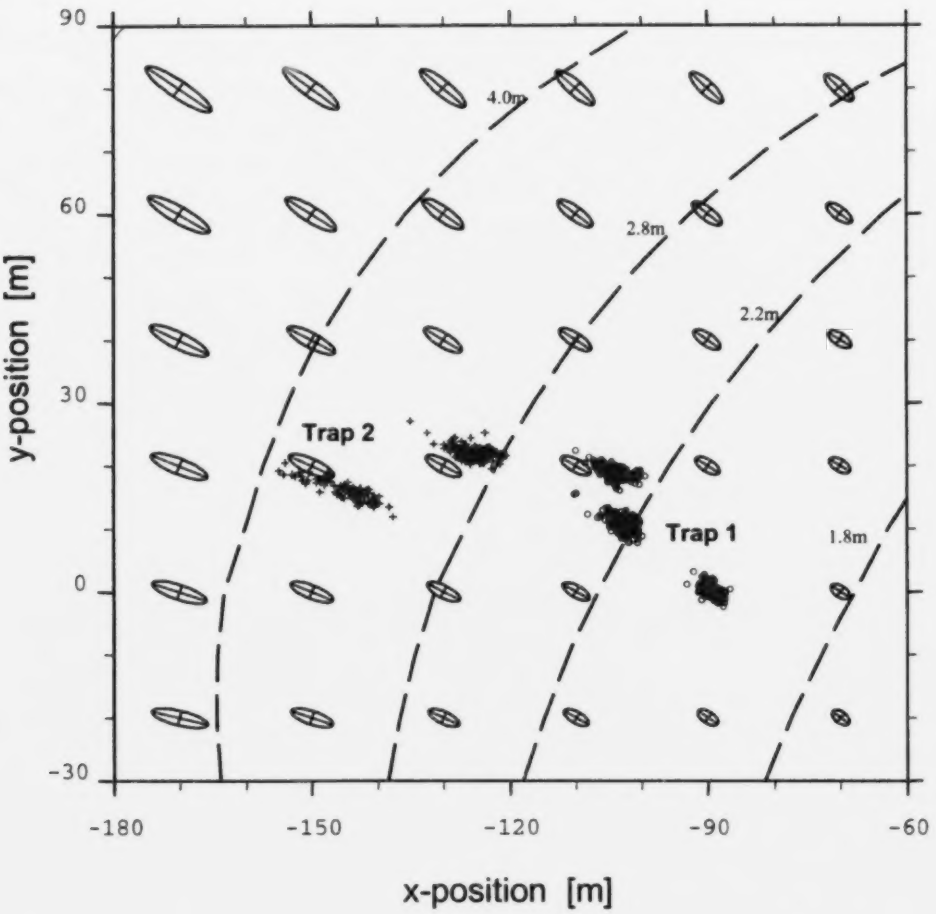

Fig. 3. Comparison between calculated positions for pingers fixed to traps (deployed in five locations) and principal axis positional errors caused by buoy movements and not accounted for in calculations. Crosses are for Trap 1, open circles for Trap 2. Contours for the length of the semi-major axis are also shown.

Lobster territories and diurnal movements

The two lobsters with the greatest number of position fixes (Lobsters 1 and 2, Table 1) remained within an area of about 160 m by 120 m just to the east of the buoy array (Fig. 4). The two territories overlapped, each roughly circular with a diameter of about 100 m. This was an area of mud-sand with cobbles and boulders in the shallower portion (2-4 m). This coarse bottom appeared to offer shelters into which the lobsters retreated at mid-day . During the day there were frequently periods of signal loss when the location of the lobsters could not be determined. This could be because the lobsters were out of range or that they entered shelters formed by boulders that prevented signal transmission. Comparison of the positions prior to signal loss and after signal recovery indicate the lobsters were largely stationary in the intervening periods (Fig. 5). Even after interruptions of as many as 15 hours, lobsters were less than 8 m away from the position prior to signal loss. The average reappearance distance was 4.6 m, comparable to the positional error outside of the buoy triangle (previous section). Given that lobsters moved several 100 m over the course of most days (Table 2) this small movement suggests the lobsters entered shelters prior to signal loss. Lobsters 1 and 2 did not return to the same locations day after day (Fig. 4).

Table 2. Mean daily distances (m) traveled by lobsters. Daylight defined as 0700-2000 hr; night as 2000-0700 hr. N days = 9

Lobster	Entire day mean (Standard error)	Entire day min,max	Daylight mean	Night mean
1	277.9 (30.4)	137.9, 479.6	90.3 (20.7)	187.6 (22.1)
2	350.3 (34.2)	214.0, 547.7	83.0 (17.5)	267.3 (24.2)

Lobsters 3 and 4 were out of range of the buoy system for most of the study, but moved distances similar to Lobsters 3 and 4 when they were tracked (Fig. 6). Lobster 3 entered the territory of Lobsters 1 and 2 from July 11-14; Lobster 4 was within the same territory on July 21-22 (Fig. 6).

Mean distance moved per 24 h period was 278 m for Lobster 1 and 350 m for Lobster 2 (Table 2). Night occurred from 2000-0700 hr when defined as the period when light intensities were 0-5% of the maximum intensity (Fig. 7). During the 11 h of night the mean distances moved were188 m (Lobster 1) and 267 m (Lobster 2); during the 13 h of daylight the mean distances moved were 90 and 83 m (Table 2). Mean distance moved per hour was linked with the light cycle (Fig. 7). Maximum light intensities were usually in the mid-afternoon, and during this period activity was reduced. Correlation between distance moved per hour and light level was significant for both Lobsters 1 and 2 ($r = 0.21$, $p < 0.05$; $r = 0.33$, $p < 0.0005$).

Current velocities during the measurement period were low (mean of hourly means = 1.6 cm sec-1). Unlike light, hourly mean current velocity was not significantly correlated with distance moved per hour for either of Lobsters 1 and 2.

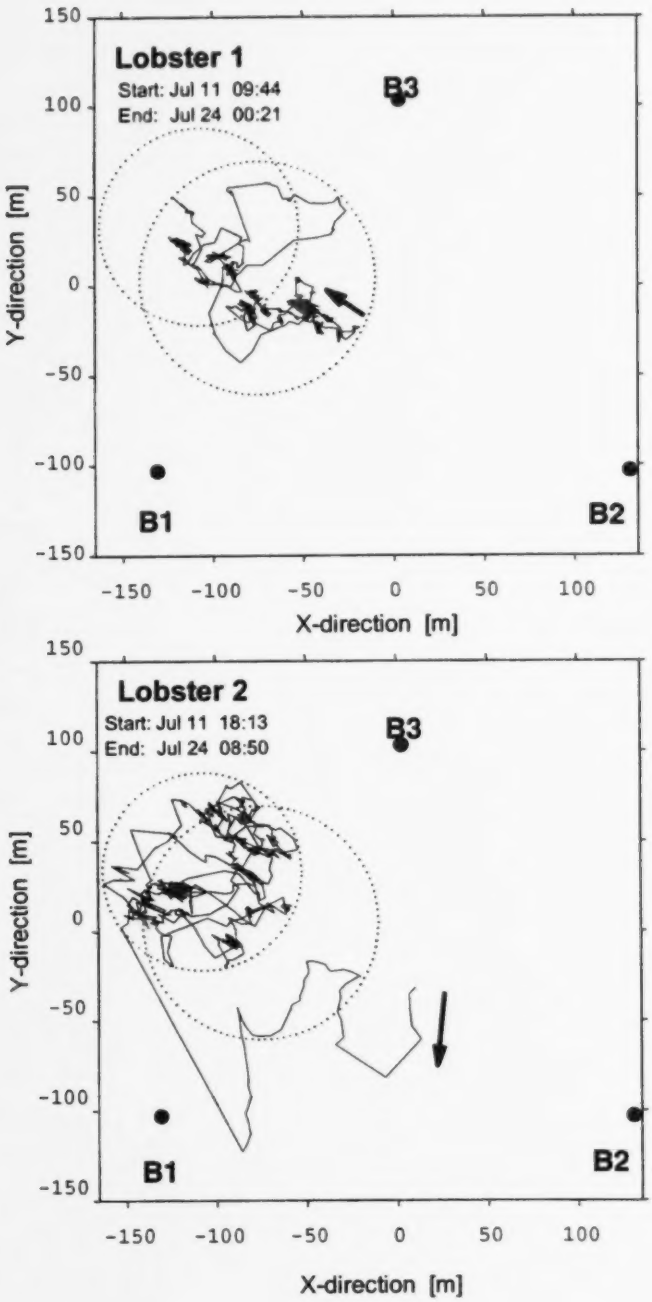

Fig. 4. Tracks of Lobsters 1 and 2 in relation to buoy positions. Arrows show where lobsters were released after the acoustic pinger was attached.

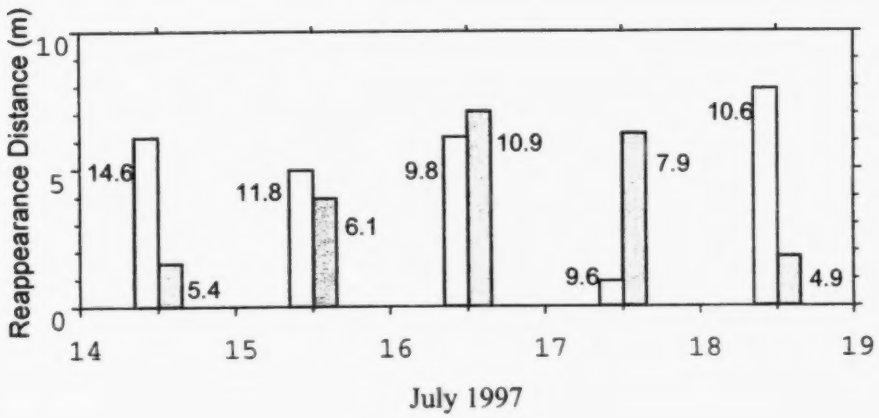

Fig. 5. Analysis of lobster movement during periods of signal loss. White bar is for Lobster 2, black bar for Lobster 1. Reappearance distance is the distance between the loss position (last calculated position before signal loss) and the reappearance position (first position calculated after signal reappearance). Numbers beside each bar represent the hours of signal disappearance.

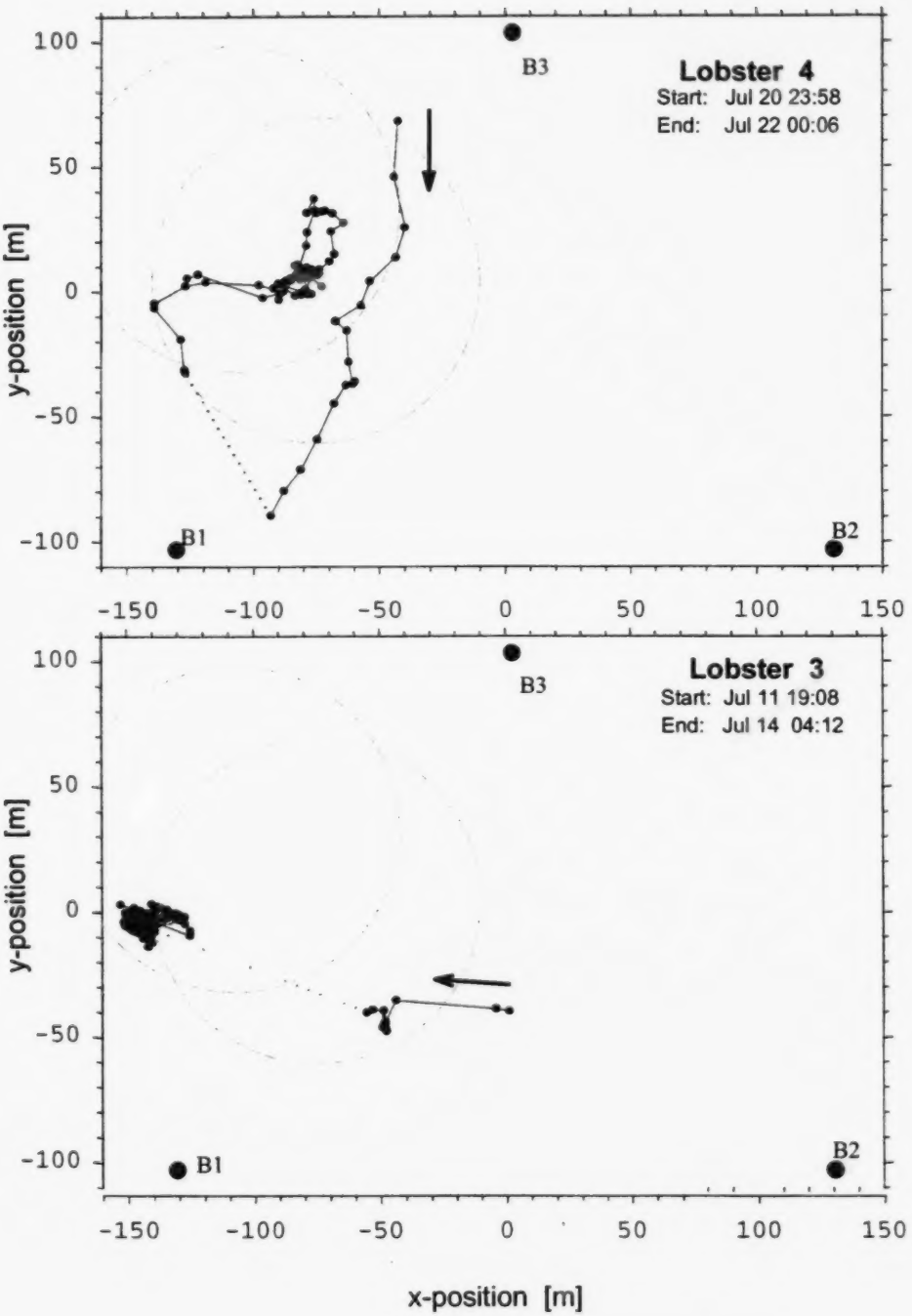

Fig. 6. Tracks of Lobsters 3 and 4 when their pingers were detectable by the buoy array. Also shown are estimated territories for Lobsters 1 and 2.

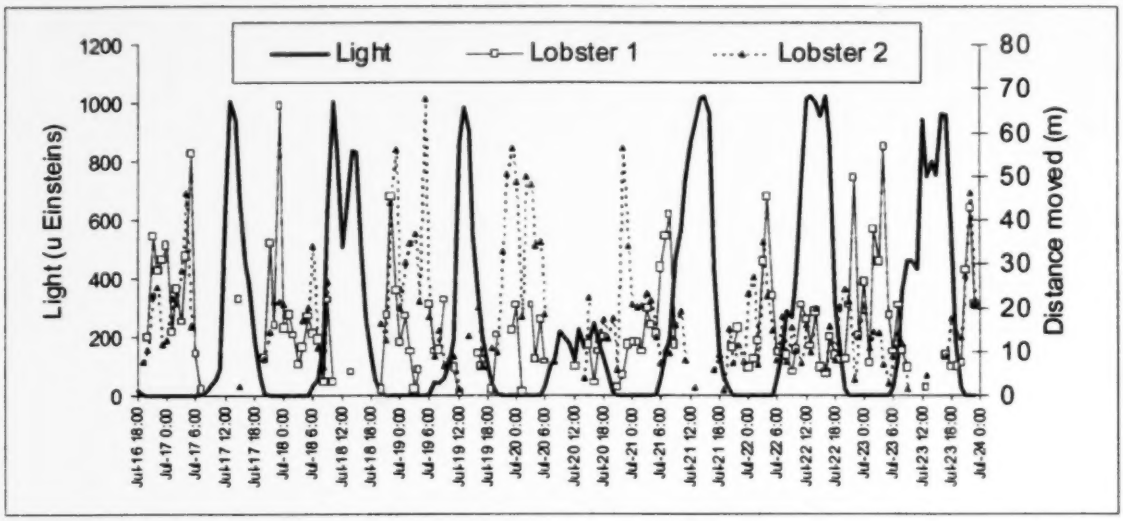

Fig. 7. Ambient light intensity and distances moved per hour by Lobsters 1 and 2.

Lobster movements and trapping

Over the three different overnight trials when traps were placed in the lobster territories, there were five occasions when a lobster was within 10 m or less of a trap but on only one occasion did a lobster actually remain in the trap. On the first night the two lobsters started out in the same vicinity and Lobster 1 traveled to within 10 m of the trap with no indication that it detected the trap (Fig. 8a). Lobster 2 was largely stationary throughout the night. On the next day the trap was reset and an additional trap was set (Fig. 8b). Lobster 1 was again less than 10 m from one trap and did not proceed towards it, travelling instead in an 80 m loop to return within 5 m of the trap by mid-morning. Lobster 2 was again stationary. On the third afternoon the two traps were reset (Fig. 8c), and that evening Lobster 1 passed close to Trap 1. Given the overlap of the track of Lobster 1 and the Trap 2 positions, Lobster 1 may in fact have entered the trap and escaped. Trap 2 had been placed within 5 m of Lobster 2 and at 2130 hr it moved towards the trap. Lobster 2 entered Trap 2 sometime later and was still present the next morning when the trap was hauled.

In the 10 traps set at the end of the experiment, a total of four lobsters were captured (Lobster 2, plus three untagged lobsters: a 78 mm CL male, an 87 mm CL female and a 100 mm CL female). The traps also captured approximately 50 rock crab and two green crab.

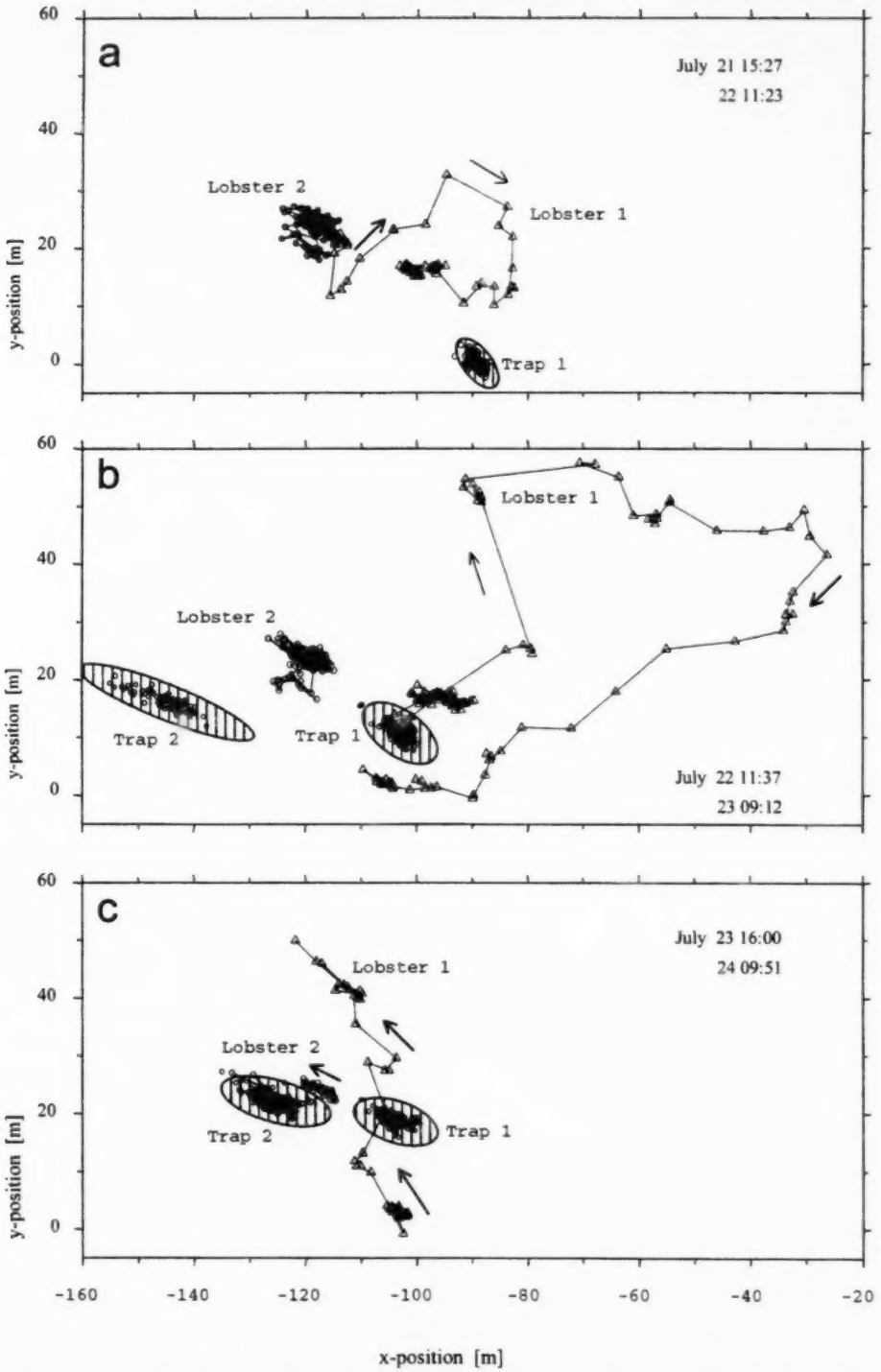

Fig. 8. Lobster tracks in relation to calculated trap positions. Each panel represents one of the three trap deployments. Trap positions (enclosed by shaded ellipses) vary because of error associated with buoy movement (see Fig. 2). Lobster 1 passed close enough to enter Trap 1 in (b) and (c); Lobster 2 was captured in Trap 2 in (c).

DISCUSSION

RAPT system and application to benthic crustaceans

The RAPT system is capable of detecting lobster movements of as small as 1 m in the center of the buoy array. Fixed pingers are recommended to evaluate the positioning error, which increases away from the centre of the buoy array and with any movement of the buoys caused by wind and currents. It is encouraging that even with the error it was possible to track the approach and entry of a lobster into a trap placed outside of the buoy array, some 130 m from the centre. It would be difficult to obtain observations remotely at this resolution with other methods.

Any effects of the pinger on lobster behavior were not evaluated here. Others have examined potential effects of pingers attached to lobsters (Watson et al. 1999) and to crabs (Hines et al. 1995) and have observed no obvious effects. Observations by Jarvis (1989) support the assumption of insignificant behavioral effects of pingers, at least for larger lobsters. Ovigerous females 98-120 mm CL tagged with pingers were observed to move several km over two months, to extrude eggs successfully, and to molt in the same manner as untagged females.

The number of lobsters tagged in this study was low, but compared to previous ultrasonic tracking studies, resolution was very high. Higher resolution was manifested both temporally (99 or more position fixes per day) and spatially ($\pm$ a few metres). Signal loss during the day was interpreted to be the result of shelter-seeking behavior of lobsters in the coarse bottom habitat. This interpretation is based on analysis of positions before and after signal interruption. Although this interpretation is not unequivocal, it is supported by diver observations at the end of the study of one of the tagged lobsters retreating to the spaces between boulders when approached.

Day-night cycle and small-scale lobster movements

Observations of a day-night cycle in lobster activity are not new but this paper provides a clear demonstration of a strong pattern for individual lobsters over several weeks. The lobsters in this study were far from inactive during daylight, but bursts of high activity were limited to night. With the high temporal and spatial resolution of the RAPT system, it would be possible to test the strength of the day-night activity cycle in different environments and for different lobster sizes. Currents were shown to be insignificant in the present study, but in some areas with higher current, lobsters have been observed foraging more during slack tide, regardless of light level (Lawton and Lavalli 1995). Daytime foraging may also be more important in areas with higher density (trade off between predation risk and food requirements) and among larger lobsters that are less likely to be preyed upon. Although Lobsters 1 and 2 stayed within relatively small areas over the two weeks, they did not appear to re-use shelters on subsequent days as has been observed for lobsters of this size elsewhere (Karnofsky et al. 1989). This may be because the tagged lobsters were only temporary residents of the area, or perhaps because of competition from other lobsters in the area.

Estimates of daily distance moved by lobsters depend both on the individual lobster's current "movement mode" and the methods of observation. Three scales or modes of lobster movement were recognized in a Gulf of Maine estuary by Watson et al. (1999): local meandering or foraging in one area, medium distance (0.3-1.0 km) rapid excursions, and longer migrations. They reported that in summer lobsters 80-98 mm CL stayed in one area for an average of 29 days. The within area movement rate was estimated at 130 m d^{-1}; the between-area movement rate was estimated at 290 m d^{-1}. Other estimates of daily movements are 463-561 m for lobsters 62-96 mm CL in summer (Lund et al. 1973), 157 and 830 m for two lobsters (65 and 73 mm CL) in November (Maynard and Conan 1984), and 300-3000 m d^{-1} for large ovigerous lobsters in summer (O'Dor and Webber 1991). These estimates were hampered by the accuracy and the number of position fixes possible in a day. In the current study Lobsters 1 and 2 were in local foraging mode, and the mean movement rates (278 and 350 m d^{-1}) were intermediate to the above studies. While the present study provides accurate estimates of daily movement rates for two lobsters, they represent only a small portion of the lobster population in the area, and variability in lobster movement rates are likely related to a host of biological and environmental factors. Ovigerous females for example move to certain locations for hatching in Jeddore Harbour (Jarvis 1989). Influences of size, sex and reproductive condition can be difficult to detect however (Watson et al. 1999). The potential for individual variability represents a challenge to studies of lobster movement behavior.

The relatively small area occupied by Lobster 1 and 2 cannot be considered a territory in the sense that it was defended, since other lobsters were in the same areas. We know this from the fact that the two other lobsters that were tagged entered the areas for several days, and that other lobsters were trapped in the area at the end of the experiment. A coarse estimate of the densities of lobsters in the area is possible from catchability coefficients (q) estimated for another area in June (Lobster Bay N.S., Tremblay and Smith 2001). For the males and females between 70 and 100 mm CL, estimated q's ranged from 189-726 m^2 per trap. Based on the observed catch rate (0.4 lobsters per trap) densities in the Jeddore study area are estimated to have been 0.0006-0.0021 m^{-2} (no m^{-2} = no $trap^{-1}$/q), yielding an estimate of 12-40 lobsters in the 160 by 120 m area occupied by the two tagged lobsters. It would be of interest to examine local foraging areas of lobsters in areas of higher density. Lobster Bay N.S. for example, has densities that are at least 20 times greater than the estimated range for Jeddore (Tremblay and Smith 2001).

Lobsters came within 10 m or less of a trap on five occasions with only one capture. A low capture rate and one that is difficult to predict for individual lobsters is characteristic of trapping studies (Karnofsky and Price 1989). While catchability coefficients are available for different areas, seasons and habitats (Miller 1995; Tremblay and Smith 2001), prediction of whether an individual lobster will enter a trap will remain difficult. The area from which a baited lobster trap draws is a function of the area covered by the bait odour plume, the sensory ability of lobsters to detect the plume, and the size of the lobster foraging area. A lobster may be out of range of a bait odour plume, but could wander within range during the nightly foraging travels of several hundred metres observed in the present study. There are no measures of how far away a lobster can detect and follow a bait odour plume, but the recent study of *Cancer pagurus* trap responses (Skajaa et al. 1998) indicates bait odour detection is

possible from distances of up to 48 m. The processes involved in the entry of lobsters and other decapods to baited traps are complex and would benefit from spatial models incorporating physical effects on the shape and spread of the bait odour plume (e.g. current speed, bottom roughness) and biological factors such as bait odour detection, and the size of foraging areas. The RAPT system provides a powerful tool for field studies related to trap-related behaviors.

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